The effect of brownification on lake phytoplankton communities in the last decades

Master thesis by Lena Huovinen

Supervision: Dr. Satu Estlander, Dr. Kristiina Vuorio, Prof. Jukka Horppila

HELSINGIN YLIOPISTO
HELSINGFORS UNIVERSITET
UNIVERSITY OF HELSINKI

SYKE
Suomen ympäristökeskus

Abstract

Faculty: Faculty of Biological and Environmental Sciences

Degree programme: Master's programme in Ecology and Evolutionary Biology

Study track: Ecology and Evolutionary Biology

Author: Lena Huovinen

Title: The effect of brownification on lake phytoplankton communities in the last decades

Level: Master's thesis

Month and year: July 2021

Number of pages: 34+1

Keywords: community ecology, lake brownification, phytoplankton, DOC, algae, freshwater

Where deposited: Helsinki University library

Abstract:

Lake ecosystems are shaped by water chemistry processes that affect the lake environment and the species communities within. Changes in the water chemistry thus have far-reaching consequences. Water colour is one variable that affects water chemistry and stems from humic substances in the water. Dark water reduces light availability and also affects nutrient and oxygen availability. A trend of brownification of freshwater systems has been observed in recent years and it is expected to influence species community's diversity and composition. The aim of this thesis was to study whether brownification is an ongoing issue in the study lakes and whether it has had a negative effect on phytoplankton diversity and resulted in shifts in the phytoplankton composition. A data set including about a 100 lakes in Finland with measurements from 1965 up until now served as the study system which was analysed with statistical methods. The results indicated a brownification trend in the past decades. The brownification so far had a positive impact on species richness but a negative impact on beta diversity. Brownification also affected species composition. Flagellates and autotrophic species increased in darker waters but mixotrophic species that are known to dominate in dark water colour, did not show a clear increase with water colour. Other hydrological variables than water colour could have had a bigger impact on the phytoplankton community than water colour but future monitoring of the phytoplankton community is recommended to see if water colour will have a negative impact on species diversity in the future.

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1. Introduction

1.1 Humic substances

Lake ecosystems are shaped by internal water chemistry processes that have an impact on the chemical and physical environment and biological processes (Moss, 2010). Lake ecosystems are thought to have a high degree of predictability because they have similar conditions to islands which means, they have boundaries that are defined more clearly than in many other ecosystems. Nevertheless, lake ecosystems can change due to environmental influences (Lampert & Sommer, 2007b). Well-studied examples of variables that affect lake ecosystems are phosphate and nitrate. Eutrophication that is caused by the increased nutrient concentration, leads to increased primary production in form of algal blooms (Schindler, 1974). Another environmental variable that has an impact on lake ecosystems is humic substances. Humic substances are naturally occurring organic substances with high molecular weight and refractory (Aiken, 1985). They are heterogeneous compounds with no exact chemical structure that are made up of a mixture of hundreds to thousands of organic compounds. The carboxylic acid groups in the humic substances increase solubility and are therefore affecting water chemistry (Keskitalo & Eloranta, 1999a). Because of their strong absorption and binding qualities, humic substances can have an impact on nutrient and oxygen availability (Keskitalo & Eloranta, 1999c; Couture et al., 2015). Due to their yellow to brown colour when dissolved in water, the humic substances lead to a dark water colour (Aiken, 1985). The dark water colour affects light availability because dark water leads to higher absorption of light. In polyhumic lakes with high contents of humic substances, only red light is still available at one-meter depth, while the rest of the light spectrum is absorbed (Keskitalo & Eloranta, 1999c). Additionally, humic substances affect thermal stratification as a result of the reduced light penetration, as the available radiation energy from light penetration is distributed to less area in a polyhumic lake than a clear water lake (Keskitalo & Eloranta, 1999c).

The humic substances are part of the dissolved organic matter (DOM). DOM consists not only of carbon but also of all other elements found in organic matter, for example, hydrogen, nitrogen and oxygen (Moody & Worrall, 2017). Different measures account for DOM. One of them is DOC and stands for dissolved organic carbon which is defined as the fraction of organic carbon that will pass through a 0.45 µm filter (Moss, 2010). The unfiltered water is defined as total organic carbon (TOC) (Keskitalo & Eloranta, 1999a). DOM has autochthonous and allochthonous sources. DOM sourced within the lake can result from excretion, cell breakdown or microbial decomposition of dead material (Lampert & Sommer, 2007a). The primary allochthonous source of organic carbon in the water is terrestrial ecosystems. Organic matter is decomposed naturally in those ecosystems and runs off into neighbouring freshwater systems (Thurman, 1985; Moss, 2010). Especially, wetlands are a dominant

source of organic matter runoff. With the high water content in the soil, organic matter leaching into downstream waters is facilitated by subsurface runoff (Keskitalo & Eloranta, 1999d; Rantakari et al., 2004). The organic matter in the water is further broken down by aquatic bacteria and serves as an energy and carbon source for them (Lampert & Sommer, 2007b).

The organic carbon in water samples can be accurately measured by carbon analysers. Water colour has been used as an approximation for dissolved organic carbon. Since a high concentration of humic substances leads to darkening of the water, DOC and water colour have been shown to be strongly positively correlated (Kortelainen, 1993; Underwood et al., 1998). But water colour can also be affected by other variables than humic substances. For example, dissolved iron and manganese result in a red-brown colour of the water (bin Jusoh et al., 2005). Also, high plankton density and silt turbidity have been shown to affect the water colour (Eloranta, 1978). Water colour is measured by using colour comparators. It is based on the principle of visually comparing the water sample to a known concentration of chloroplatinate solution (g m^{-3} Pt) and scaling it upon that (Hazen, 1892). This method has been used for a longer period of time which means there are data available dating decades back. More accurate measurements are made with a colourimeter or spectrophotometer (Keskitalo & Eloranta, 1999b).

Humic lakes with dark water colour and high organic carbon concentration are common in temperate and cold regions in the boreal zone. Finland is a prime example of a region that has many humic lakes (Kortelainen, 1993). The country has an extensive freshwater system with at least 29’515 lakes with a surface area over 0.04 km^2 with a mean of 12 g m^{-3} in TOC and 100 g m^{-3} Pt in 1987 (Keskitalo & Eloranta, 1999d). Since Finland has the highest proportion of peatland to land in the world, the high DOC concentrations in Finnish lakes can be seen as a result of the surrounding catchment of those lakes. Catchment has been shown to be an important variable for TOC concentration in Finnish lakes. In large lakes, water bodies and peatland water in the catchment area explained most of the variation in TOC, while water and latitude explained most of the variation in small lakes (Rantakari et al., 2004).

1.2 Changes in humic lakes

In recent years, an increase in DOC concentration, occasionally referred to as brownification, has been observed in Europe and North America (Garmo et al., 2020). Also in Finland, an increase in DOC concentration has been observed in small forest lakes (Vuorenmaa et al., 2006). This increase could be caused by climate change. A warming climate increases the decomposition of peatlands, one of the primary sources for the DOC (Freeman et al., 2001, 2004). Another reason for increased decomposition is the impact of the draining of peatland inflicted by humans. The draining leads to increased aeration which facilitates peat decomposition (Minkkinen et al., 1998; Laine et al., 2013). Additionally to the increased decomposition, increased water discharge from the peatlands also resulted in a higher DOC

concentration (Pastor et al., 2003). Changes in the precipitation patterns can lead to increased discharge which also can be seen in the DOC fluctuation during the year (Lenard & Ejankowski, 2017). This humic stress is expected to have impacted species communities in recent years and will continue in the future if this brownification of freshwater systems continues. Warming and increased browning are expected to decrease phytoplankton diversity (Urrutia-Cordero et al., 2017) and dark water colour has been related with low species richness (Eloranta, 1995). Therefore, the increased humic stress could have a negative impact on phytoplankton diversity.

1.3 Effects on species community

Since the concentration of humic substances affects water chemistry in lakes, it also influences the species community and biological interactions within those communities. Dissolved organic carbon can be a selective agent on community composition and population levels (Robidoux et al., 2015). Phytoplankton is at the basis of the food web because it assimilates inorganic carbon in the pelagic zone and is therefore the source of primary production in the lakes. Thus, changes in the phytoplankton community can have far-reaching consequences on the whole lake ecosystem (Ask et al., 2009).

DOM from allochthonous sources is related to a decrease of energy mobilization in the benthic and pelagic zone, as light penetration decreases in darker waters. In unproductive lakes the primary production shifts from the benthic to the pelagic zone along a gradient of DOC. Therefore, humic lakes are expected to be dominated by pelagic mixotrophs in contrast to clear water lakes that are expected to be dominated by benthic autotrophs (Ask et al., 2009). The change in the nutritional mode in phytoplankton communities is related to the smaller volume of the upper illuminated layers in lakes, where mixotrophic species are outcompeted by autotrophic species. Mixotrophic species are less dependent on light and respond better to the low light conditions implied by high DOC concentrations (Lebret et al., 2018). Since brownification also leads to a reduced volume of illuminated water layer tracking favourable conditions can be an advantage. Flagellated species have increased motility, as they are capable of directed movement (Clegg et al., 2007). Therefore flagellated species are expected to dominate over non-flagellated species in water with high DOC concentrations (Deininger et al., 2017). DOC also has effects on zooplankton. Organic carbon can be a resource for zooplankton and promote bacterial growth (Cole et al., 2011), and has an impact on zooplankton traits. Due to decreased visibility in lakes with high DOC concentration, zooplankton may shift to larger species, since the detection by predators is hindered by the decreased visibility (Wissel et al., 2003). The community structure in phytoplankton and zooplankton will also further affect the other species, for example, their direct predators. Thus, changes in the input of humic substances have not only impacts on water

chemistry, which further influences the chemical and physical environment, but also on all biological communities and interactions.

1.4 Aim of the thesis

Previous studies looked at the short-term effects of brownification on the phytoplankton species community. The long-term effect is therefore not yet fully understood. This thesis aims at studying how brownification affects the lake phytoplankton community over decades. The first aim was to study whether the organic carbon and water colour changes in about a hundred study lakes in Finland are comparable to the globally observed increasing trend. Additionally to brownification, other water chemistry and lake property variables were included to consider other changes in water chemistry that have occurred in the study lakes. The second aim of the thesis was to study if water chemistry changes reduced phytoplankton biodiversity. The third aim was to determine whether changes in water colour led to a shift in community composition towards mixotrophic and flagellated species that are expected to dominate in dark colour conditions.

2. Material and Methods

2.1 Data

The data used in this thesis consisted of two different data sets. The starting point was a data set provided by Kristiina Vuorio of the Finnish Environment Institute (SYKE). The data is part of the RNA-unit project by the University of Jyväskylä that sampled 103 lakes in Southern and Middle Finland (Figure 1). 115 water samples were taken in 2014 and 2015 during late June, July and August from the surface down to two-meter depth. Additionally, the temperature and Secchi depth were taken on site. The samples were then analysed by SYKE for water colour and showed a variability from 10 to 240 mg Pt L^{-1} across the lakes studied. In addition to water colour, total phosphorous, nitrate and DOC were also detected. The phytoplankton community in the samples was identified by different people and consisted of the number of counted units and biomass per litre (Table 1). The data also included information on the functionality of the phytoplankton species, specifically about nutritional mode (autotrophic/mixotrophic) and movement type (flagellated or non-flagellated).

Table 1: Description of variables in the dataset.

Variable	Description	Distribution
Water colour	Water colour is scaled with a colour comparator with a comparison to a known concentration of chloroplatinate solution (mg Pt L-1). The exact methods are unknown.	10 - 240 mg Pt L-1, mean = 72.8 mg Pt L-1

DOC	The dissolved organic carbon was analysed in a carbon analyser. The exact methods are unknown	5 - 17.4 mg L-1 , mean = 10.55 mg L-1
Total phosphorous, unfiltered	The total phosphorous was analysed by flow analysis. Standard = ISO/DIS 15681-2	3-173 µg L-1, mean = 19.19
Total nitrogen, unfiltered	The total nitrogen was detected by manual vanadium(III) reduction, Standard = SFS – EN ISO 13395. The measurement is performed with a Gallery Plus discrete device.	292-1655 µg L-1, mean = 565.73 µg L-1

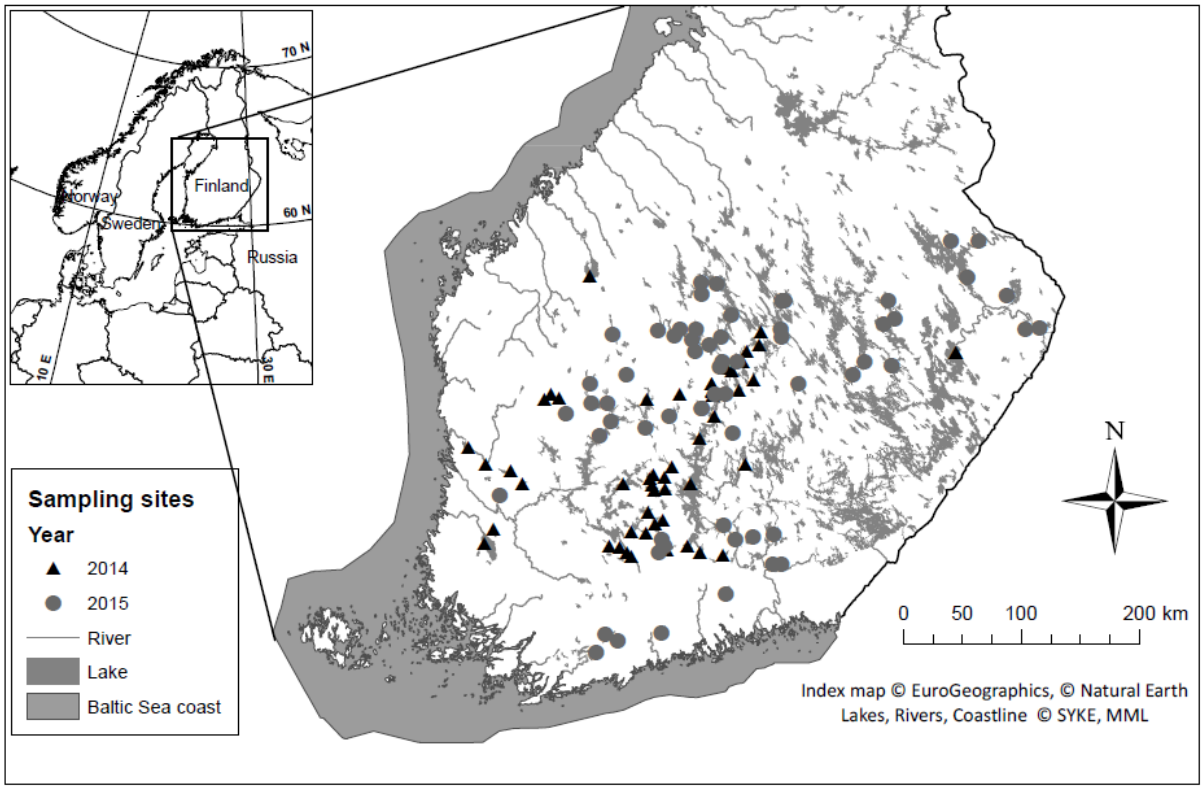

Figure 1: Locations of the 103 sample sites of the RNA-unit project by the University of Jyväskylä.

To study long-term effects in the lake ecosystems, additional data was acquired from the open databases of SYKE. The surface water database and the phytoplankton database were used. The data for the water chemistry analysis was from the surface water database and included measurements from 1965 to 2020. The first extensive water sampling program by authorities was conducted in 1963 and later repeated in 1965 (Heinonen, 1980), in which most of the lakes had been sampled that were later studied by the RNA-unit project. After 1965 measurements were repeated independently from the lake survey until today in most of the lakes. The number of measurements available for the lakes varies greatly. Within this timeframe, all available measurements in August and at one-meter depth were included in the dataset to reduce variation in the phytoplankton community. The dataset

consisted of the same water chemistry data as the RNA-unit project, but the methods used while producing the data are unknown. The water chemistry consisted of water colour, temperature, total phosphorous, total nitrogen, DOC, iron, and TOC. Phytoplankton abundance data was sourced from the phytoplankton database in biomass per litre. General information on lake properties is also available in both databases of SYKE, so water area, maximal depth and catchment area were also added from there. The data from the open databases have been captured by different people and organisations, thus it might vary in quality.

In addition to this broad data set, one lake was chosen for closer examination in terms of a case study. The choice was made for lake Päijänne. Lake Päijänne is a big and deep lake that is separated into different basins (Figure 2). Because of its importance as a drinking water reservoir for a large area in Finland, there is a series of data at different sample sites available (Table 2) which enables close monitoring of the lake's water quality (Forsius et al., 2017). Lake Päijänne has a history of eutrophication and pollution (Granberg, 1973) but is originally thought to be an oligotrophic lake (Jaernefelt, 1956). Hence the water colour values are low compared to other lakes in the study area.

Table 2: Properties of the sample sites in Lake Päijänne.

Sample site	Site depth (m)	Water area (ha)	Catchment area (ha)	Water colour 2015 (mg/L*Pt)	Coordinates ETRS-TM35FIN
Päijänne 69,	41,5	14108	NA	40	6894998-437115
Päijänne 70, Ristinselkä	76.1	14109	153481	40	6882354-435805
Päijänne 71, Vanhanselkä	66	86487	1382874	40	6864256-423390
Päijänne 740, Tehinselkä	36	86487	32749	40	6864256-423390

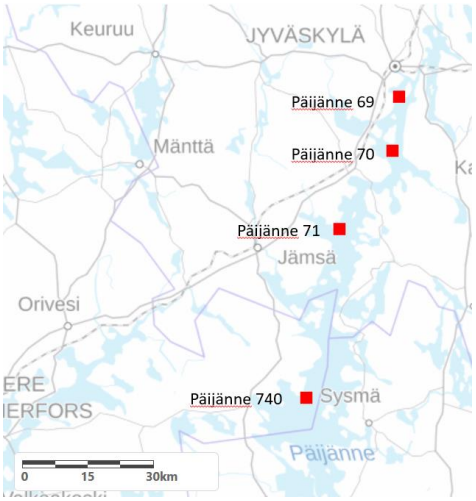

Figure 2: Sample sites in lake Päijänne

2.2 Biodiversity

In order to test the effect of long-term brownification on lake plankton communities, species richness and turnover were calculated to account for changes in the number of species present and community composition (see below).

For the broad data set of sampled lakes, diversity indices were calculated based on species abundance data that was available due to the Finnish lake survey and the RNA unit project, for the years 1965 and 2015. For lake Päijänne though all the measurements from the open databases that included water colour and phytoplankton abundances were used for index calculation. The data for lake Päijänne includes data taken in August from 1965 until 2019. The species data was restricted to data from August and the sampling depth of one meter to reduce variation in the community composition. The biodiversity indices were calculated between all the available time points and stored in a matrix. The same procedure was used for the water colour.

2.2.1 Richness

Species richness is a method to describe regional species diversity that can be a useful simple method for a delimited sample area and time (Magurran, 2004). Species richness acts as a downward estimator because it only represents the known species in the study area and not the actual species richness (Gotelli & Colwell, 2001). In this thesis, richness was defined as the number of species per sample. The thesis aimed to find changes in species richness and not the accurate amount of species, hence the number of species in a sample is an adequate approximation of species richness. The difference in richness between 1965 and 2015 in all lakes was calculated by subtracting the richness in 1965 from the richness in 2015.

2.2.2 Beta diversity

Beta diversity is part of a construct for spatial diversity regarding different components of species diversity. Alpha diversity represents the local diversity, beta diversity the spatial turnover and gamma diversity the regional diversity (Koleff et al., 2003). Traditionally, beta diversity is defined as beta diversity = gamma diversity/alpha diversity and was first described as "the extent of change in community composition among sites" (Whittaker, 1960). Beta diversity is therefore the difference in species composition in two or more localities. Apart from the original formulation by Whittaker, many formulas have been published for beta diversity which impedes generalizing beta diversity patterns (Koleff et al., 2003).

To understand if the phytoplankton community changed by species loss or turnover a beta diversity partitioning approach into turnover and nestedness was used. Using this approach in the master thesis could help to not only get an insight on changes in species richness among sites but also on what kind

of changes occurred in the species community. Low nestedness and high beta diversity imply that the species in the species pool were replaced due to species turnover. Nestedness is the result of ßnes = ßsor – ßsim (Baselga, 2010). The Sørensen dissimilarity index (ßsor) is a measure of beta diversity that represents true spatial turnover and differences in richness (Koleff et al., 2003). This index needs presence/absence data, as at least two patches are compared in the presence and absence of their species. The common species in both patches are related to unique species in the patches. The *a* represents the common species in both patches, *b* the species unique to the first patch and *c* the species unique to the second patch. The index ranges from zero to one, where one means that the patches have no species in common and zero means two identical patches (Sørensen, 1948). Sørensen dissimilarity index is formulated as follows:

$$ßsor = \frac{b + c}{2a + b + c}$$

The Simpson index (ßsim) was first mentioned by Simpson (1943) and later rediscovered by Lennon et al. (2001). It represents the species turnover between sites well and is not influenced by species richness gradients (Lennon et al., 2001; Baselga, 2010). The index compares the minimal common species in both patches to the common species in the patches. The variables are the same as for the Sørensen dissimilarity index, so *a* represents the common species in both patches, *b* the species unique to the first patch and *c* the species unique to the second patch. The Simpson index is formulated as follows:

$$ßsim = \frac{\min(b, c)}{a + \min(b, c)}$$

When both beta diversity indices are combined, a partition of the beta diversity can be derived. Partitioning beta diversity into nestedness and spatial turnover gives information about how the species composition changes among communities. Communities with high nestedness have a common species pool and the beta diversity changes due to the addition of new species to one patch. Low nestedness and high beta diversity imply that the species in the species pool were replaced due to species turnover. Nestedness is the result of as ßnes = ßsor – ßsim that equals to (Baselga, 2010):

$$ßnes = \frac{\max(b, c) - \min(b, c)}{2a + \min(b, c) + \max(b, c)} \times \frac{a}{a + \min(b, c)}$$

All these indices are pairwise beta diversity indices and were calculated between 1965 and 2015. This was applied under the assumption that temporal turnover can be depicted with spatial turnover, as the beta diversity indices were formulated for spatial turnover.

To analyse temporal turnover more precisely, the data for lake Päijänne was used, as it included more data points in between 1965 and 2015. The pairwise beta diversity was calculated between all available time points, resulting in a matrix.

2.3 Statistical methods

Statistical models and visualisation of the data were carried out in R version 4.0.2 (R Core Team, 2020). Different packages in R were used to analyse the data. The models included: changes in hydrology variables from 1965 to 2020, what variables affected the change in water colour, biodiversity changes between the years 1963 and 2014/15 and phytoplankton community changes from 1965 to 2020. The package ggplot2 in R was used to illustrate the data (Wickham, 2016).

2.3.1 Change in water hydrology

Overall changes

The change in the hydrology variables between 1965 and 2020 was analysed with a linear mixed effect model of the data from the SYKE databases. The model assumes a normal distribution of the data and includes fixed and random effects and accounts well for the data because of repeated sampling at the same sample sites (Bates et al., 2015). The different hydrological variables water colour, iron, temperature, TOC, total unfiltered phosphorous and total unfiltered nitrogen were related to sampling time as fixed effects and sampling site as a random effect. To get estimates for the hydrological changes in all the lakes, a linear mixed model was used with logarithmic water colour as the response variable and sample site as the fixed effect. The random effect was the sampling time as the data was taken in a time series and the colour could be affected by the previous colour numbers. The lme4 package in R was used to model and analyse the data (Bates et al., 2015).

Since a darker water colour can have different sources, the other hydrological variables were related to water colour to get an insight into which variables might have caused a change in water colour. For this, a linear mixed effect model was used with iron, temperature, TOC, total unfiltered phosphorous and total unfiltered nitrogen as fixed effects and sample site as a random effect.

To compare the overall changes to one example lake with more abundant measurement, the same statistical analysis for hydrology was conducted for a subset of the data containing only data from lake Päijänne.

2.3.2 Changes in biodiversity

To analyse the overall change in biodiversity over the time period, a linear mixed effect model was used on the data from the SYKE database with richness related to sampling time as a fixed effect and sampling site as a random effect. To analyse the effect of the changes in hydrology on biodiversity, the estimate of the hydrological change of water colour, iron, temperature, TOC, total unfiltered

phosphorous and total unfiltered nitrogen was related to richness, turnover and nestedness. For that, the beta values, that represent the slope of the regression equation, from the overall changes models were related to the pairwise beta diversity as fixed effects and the sample site as a random effect. The package lme4 in R was used to model and analyse the data.

Lake Päijänne

For lake Päijänne the matrix of pairwise beta diversity among all possible sampling times was related to a matrix of the difference in water colour. A linear regression model was used to relate the matrices of differences among sampling times in beta diversity and water colour to each other.

2.3.3 Changes in community

Changes in functionality and nutritional mode were analysed in the RNA-unit dataset. A linear mixed effect model was used and the logarithmic of motility mode (flagellated) and nutritional mode (autotrophic/mixotrophic) was related to water colour.

To analyse changes in the community composition due to changes in hydrology, a joint species distribution modelling approach was used. Joint distribution modelling does account for species and community parameters and does therefore account for community joint traits like species traits or phylogenetic relationships. The model was a multivariate hierarchical generalised linear mixed model fitted with Bayesian inference using a Markov chain Monte Carlo (MCMC) method (Abrego & Ovaskainen, in print). The analysis was done in R with the Hmsc package (Tikhonov et al., 2019). In the model, a matrix of phytoplankton abundances was estimated with probit regression and related to the hydrological variables colour number, DOC and phosphorus concentration. Two chains with 1000 samples and thinning of $\Delta s = 10$ were used to fit the model with MCMC. The phytoplankton abundances were analysed for phytoplankton groups instead of species to get a broad overview.

3. Results

3.1 Changes in water hydrology

Overall changes

There were changes in the water chemistry variables detectable during the last decades in the broad set of study lakes. On one hand, nitrogen, phosphorous, TOC and DOC decreased, on the other hand, water colour number and water temperature increased (Figure 3, Table 2). The increase in water colour was mainly caused by colour values over 200 mg Pt L-1 after the year 2000 (Figure 3). Iron and TOC were positively related to water colour, and temperature and phosphorous were negatively related to water colour. However, only the effects of TOC and phosphorous were significant (Table 3).

Table 2: Results for the linear mixed effect model for the overall hydrological change in the lake.

Variable	Beta-value	SE	P-value
Colour	$8.27 * 10^{-11}$	$7.67 * 10^{-12}$	$4.1 * 10^{-27}$
Phosphate	$-1.68 * 10^{-10}$	$8.06 * 10^{-12}$	$5.09 * 10^{-96}$
Iron	$5.16 * 10^{-11}$	$1.78 * 10^{-10}$	0.772
Nitrate	$-3.59 * 10^{-10}$	$1.02 * 10^{-10}$	$4.09* 10^{-4}$
Temperature	$6.45 * 10^{-11}$	$4.15 * 10^{-12}$	$1.63* 10^{-54}$
DOC	$-3.59 * 10^{-10}$	$1.02 * 10^{-10}$	$4.09* 10^{-4}$
TOC	$-3.41 * 10^{-11}$	$2.47 * 10^{-11}$	0.167

Table 3: Linear mixed effect model results for water colour related to the hydrological variables in the model.

Variable	Beta value	SE	P-value
Iron	0.049	0.048	0.315
Temperature	-15.092	19.540	0.440
TOC	3.820	0.512	9.92*10-14
Total phosphorous unfiltered	-0.213	0.040	3.56*10-4
Total nitrogen, unfiltered	0.022	0.005	3.88*10-6

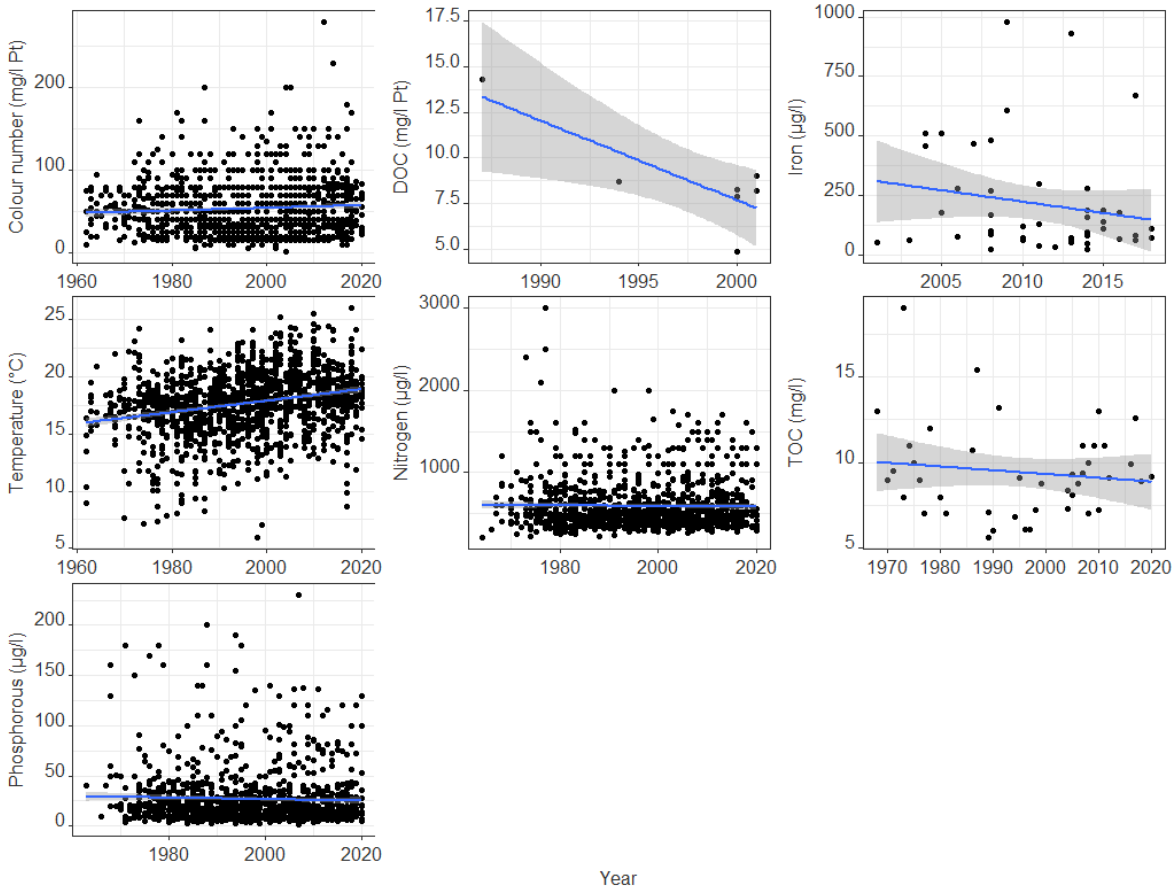

Figure 3: Hydrology trends over the last decades.

Changes in lake Päijänne

The changes in lake Päijänne were similar to the overall changes. The available variables showed a decrease in water colour, TOC and phosphorous, and an increase in temperature (Figure 4, Table 3). The water colour decreased until the year 2000 and increased thereafter (Figure 4, first panel).

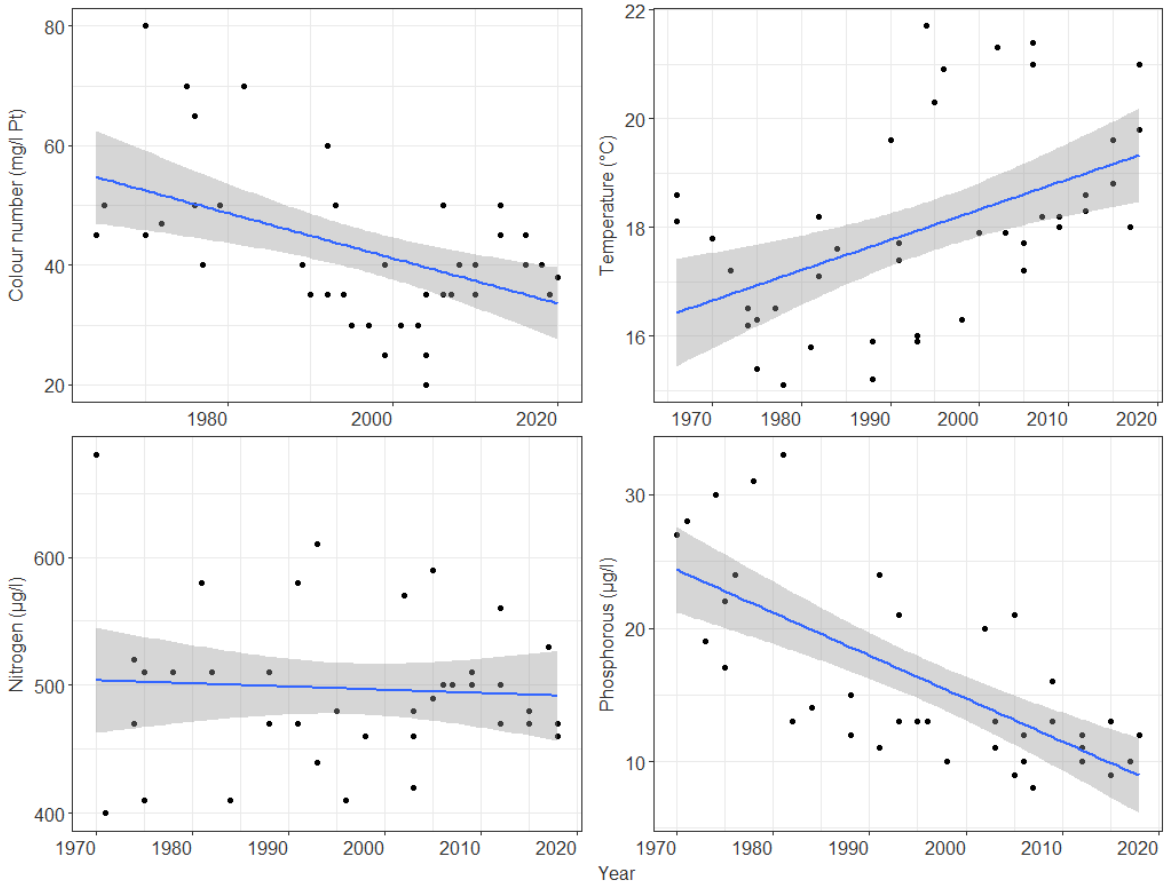

Figure 4: Changes of hydrological variables in lake Päijänne.

3.2 Biodiversity changes

Overall changes

Species richness increased from 1965 to 2015 (ß = 0.27, SE = 0.047, p-value = $1.49*10^{-8}$). From the hydrological variables, colour (Figure 5), phosphate, temperature and iron showed a positive effect on the difference in richness between 1965 and 2015. Nitrate and TOC affected the difference in species richness negatively. However, none of these effects was significant (Table 4).

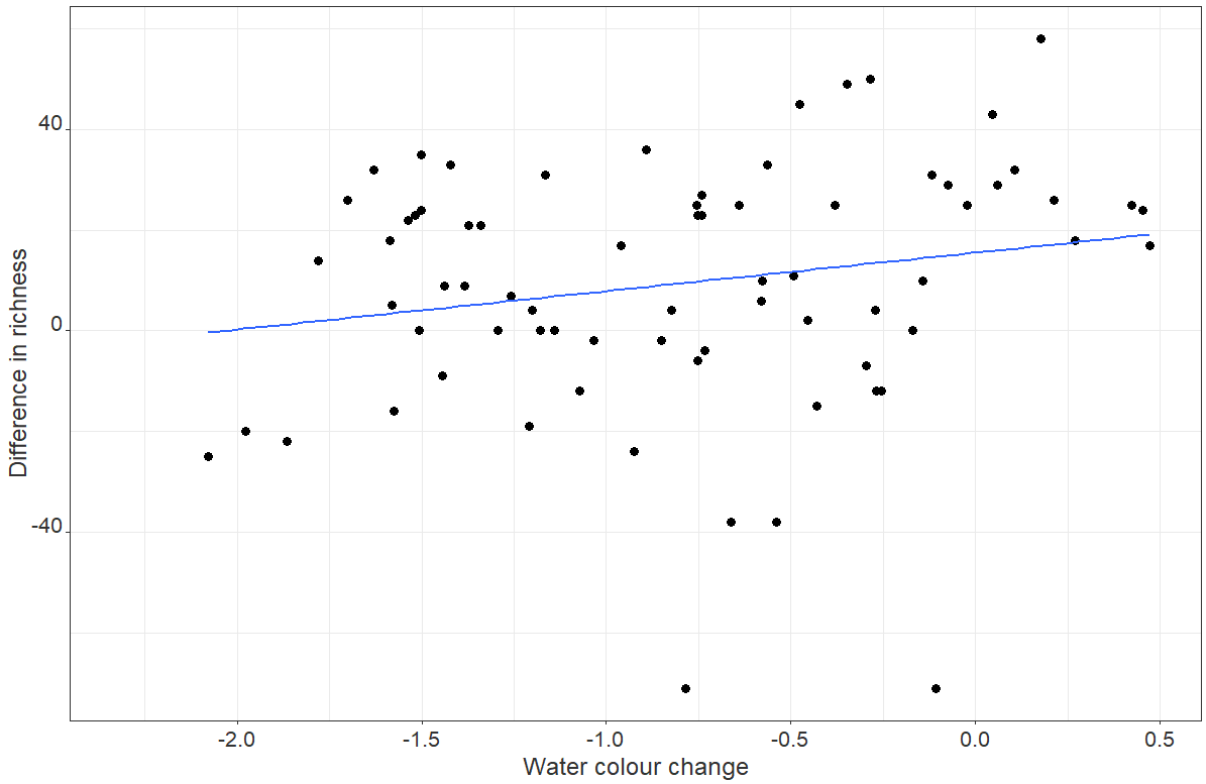

Figure 5: Change in richness between 1965 and 2015 in the lakes compared to the change in colour in the lakes.

The Simpson index was negatively affected by colour and phosphate, and positively affected by nitrate, temperature, iron and TOC. But none of these effects was significant. Overall, the Simpson values were all bigger than 0.5 (Appendix, Table 6). Nestedness was negatively affected by nitrate (p-value = 0.04) and by iron (p-value = 0.02) and positively affected by phosphate (p-value = 0.1), colour (p-value = 0.02), temperature (p-value = 0.02) and TOC (p-value = 0.02) (Table 4, Figure 6). The nestedness values in the lakes were low in general, below 20 per cent (Appendix, Table 6).

Table 4: Estimates for the relationship between change in hydrology and change in biodiversity. Linear regression models for richness (R^2= 0.997), Simpson (R^2= 0.9526) and nestedness (R^2= 0.9983).

Estimate	Beta-value	Se	P-value
Richness			
Estimate_colour	78.656	7.032	0.057
Estimate_phosphate	6.260	1.402	0.140
Estimate_nitrate	-15.107	2.1654	0.091
Estimate_temperature	467.775	29.888	0.041
Estimate_iron	15.508	0.957	0.056
Estimate_TOC	-5.869	20.068	0.772
Simpson index			
Estimate_colour	-0.013	0.054	0.849
Estimate_phosphate	-0.022	0.011	0.287

Estimate_nitrate	0.028	0.016	0.338
Estimate_temperature	0.276	0.228	0.440
Estimate_iron	0.021	0.021	0.506
Estimate_TOC	0.015	0.007	0.294
Nestedness			
Estimate_colour	0.172	0.006	0.023
Estimate_phosphate	0.008	0.001	0.100
Estimate_nitrate	-0.027	0.002	0.044
Estimate_temperature	0.856	0.026	0.019
Estimate_iron	-0.083	0.002	0.018
Estimate_TOC	0.028	0.001	0.019

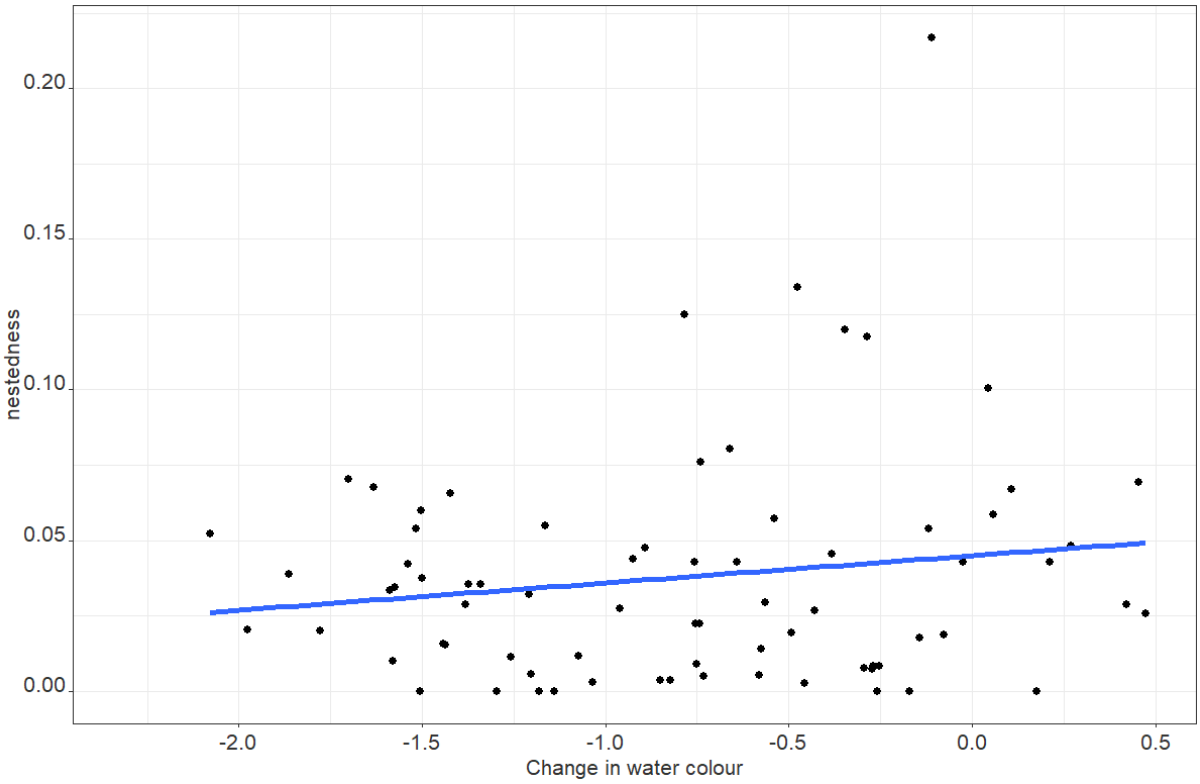

Figure 6: Change in nestedness between 1965 and 2015 in the lakes compared to the change in colour in the lakes.

Changes in lake Päijänne

In lake Päijänne higher colour classes were related to a higher richness in two out of three sample sites (Figure 7). Considering all the differences in colour and diversity among all sampling times, an increase in colour increased species richness (ß = -0.1496, SE = 0.2580, p-value = 0.5631). A higher decrease in colour increased species richness as well (Figure 8). Turnover decreased with an increase of water colour (ß = -0.008, SE = 0.001, p-value < 0.001) (Figure 8). Nestedness decreased slightly with water colour (ß = -0.0001, SE = 0.0007, p-value > 0.05) (Figure 8). However, none of those correlations were significant.

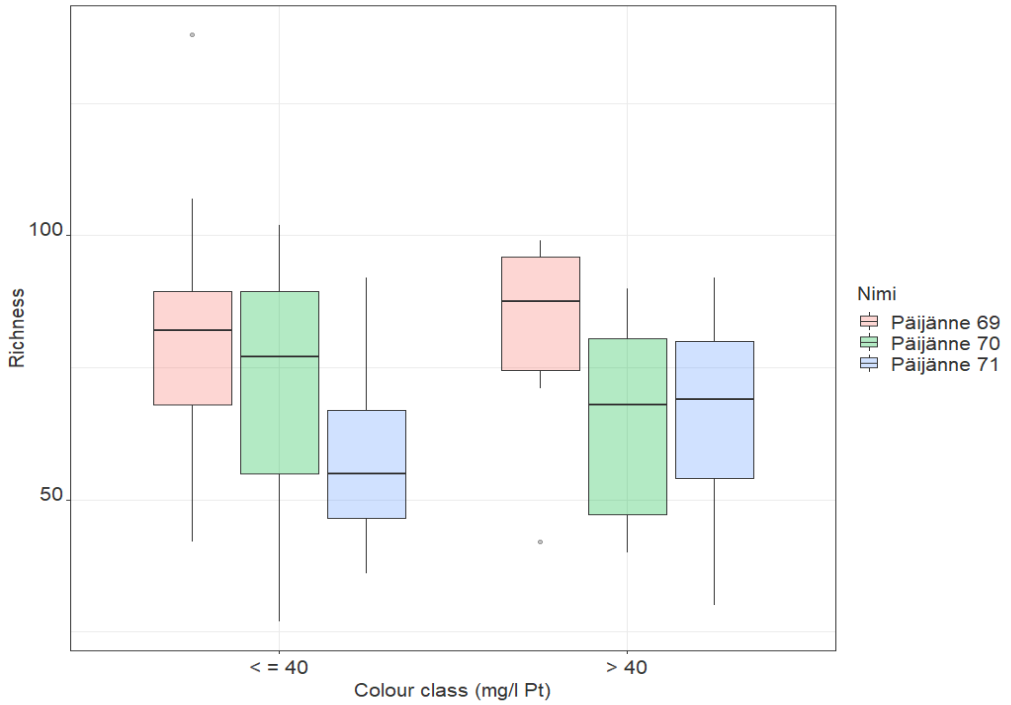

Figure 7: Species richness compared to colour in Lake Päijänne at the three sample sites Päijänne 69, Päijänne 70 and Päijänne 71.

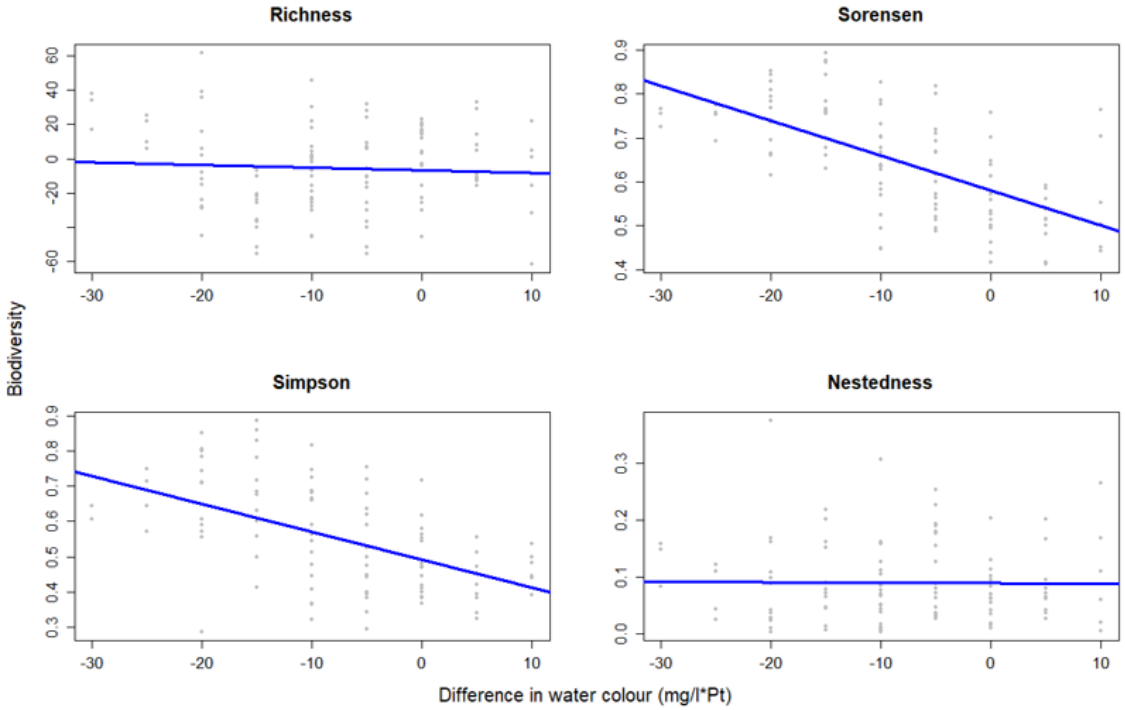

Figure 8: Beta diversity analysis for lake Päijänne at sample site 71, x-axis = differences in colour between years, y-axis differences in beta diversity between years. Difference = Euclidian distance.

3.3 Community results

The phytoplankton community from all sites from the RNA-unit data set in 2015 changed with colour. Flagellates and autotrophic species increased with colour, although not significantly (Table 5, Figure 9 & 10). Mixotrophic species decreased with colour but not significantly (Table 5, Figure 10).

Furthermore, temperature, DOC and phosphorous increased the number of flagellates significantly, while nitrogen decreased this number significantly (Table 5). DOC and phosphorous increased the number of autotrophic species significantly, while temperature and nitrate decreased it (Table 5). Temperature, DOC and phosphorous also increased the number of mixotrophic species significantly, while nitrogen decreased this number significantly (Table 5).

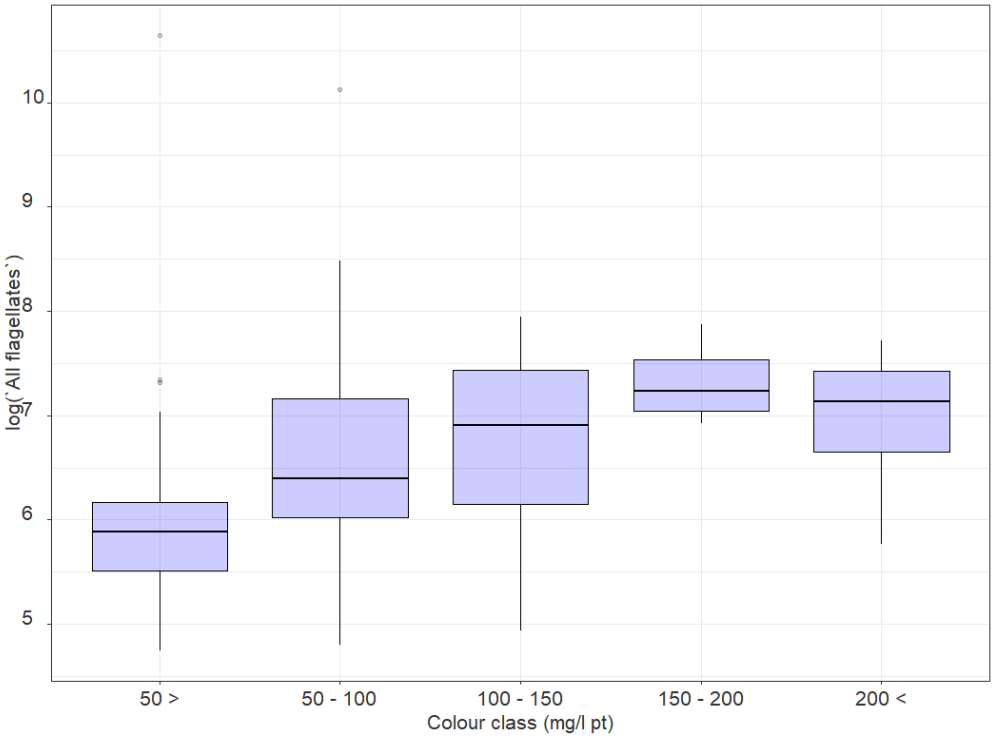

Figure 9: Number of flagellated species compared to water colour class in the sample lakes in 2015.

Table 5: Linear regression models with hydrological variables related to flagellates (R2=0.5372), autotrophs (R2=0.3918), mixotrophs (R2 = 0.5168).

Response variable Explanatory variables	**Betas**	**Se**	**P-value**
Log(Flagellates)			
Colour number	0.001	0.001	0.682
Temperature	0.072	0.026	0.007
DOC	0.081	0.030	0.008
Total phosphorous	0.048	0.005	$2.63*10^{-14}$
Total nitrogen	-0.004	0.001	$7.21*10^{-08}$
Log(Autotrophs)			
Colour number	0.004	0.002	0.080

Temperature	-0.042	0.031	0.178
DOC	0.085	0.036	0.018
Total phosphorous	0.035	0.007	$3.81*10^{-07}$
Total nitrogen	-0.003	0.001	$5.33*10^{-05}$
Log(Mixotrophs)			
Colour number	-0.003	0.002	0.157
Temperature	0.073	0.027	0.008
DOC	0.081	0.031	0.009
Total phosphorous	0.052	0.006	$3.39*10^{-15}$
Total nitrogen	-0.003	0.001	0.001

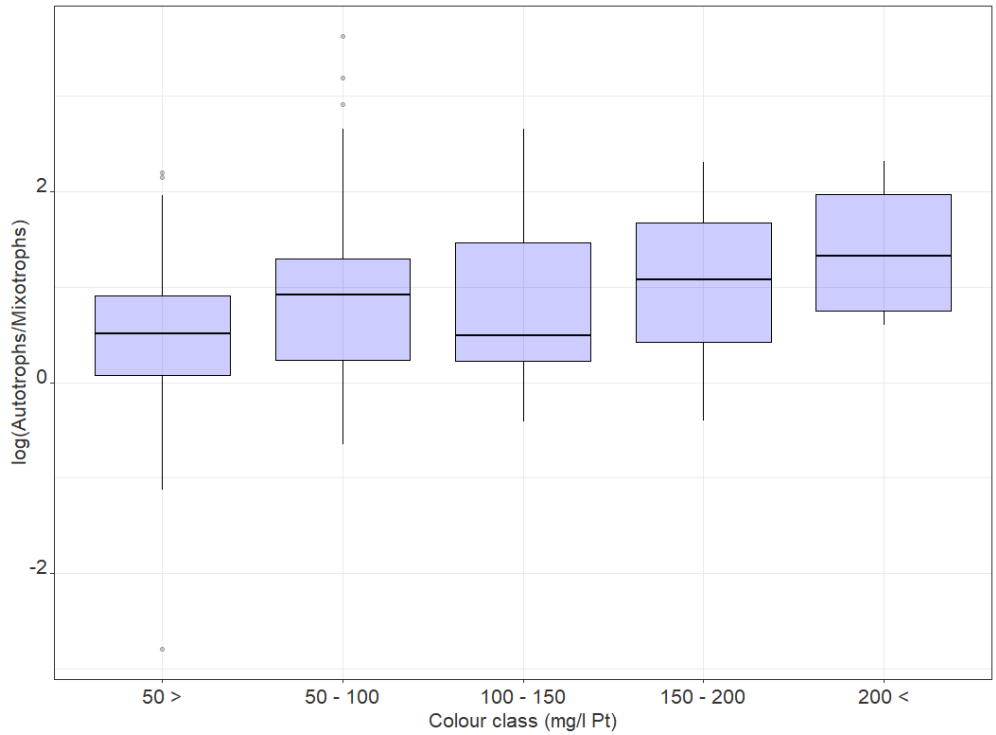

Figure 10: Ratio of autotrophic to mixotrophic species compared to water colour class in the sample lakes in 2015.

DOC was found to affect all phytoplankton classes positively. Phosphate was observed to have a negative or no effect on the phytoplankton classes. Water colour had a positive effect on all classes but the class Conjugatophyceae (Figure 11).

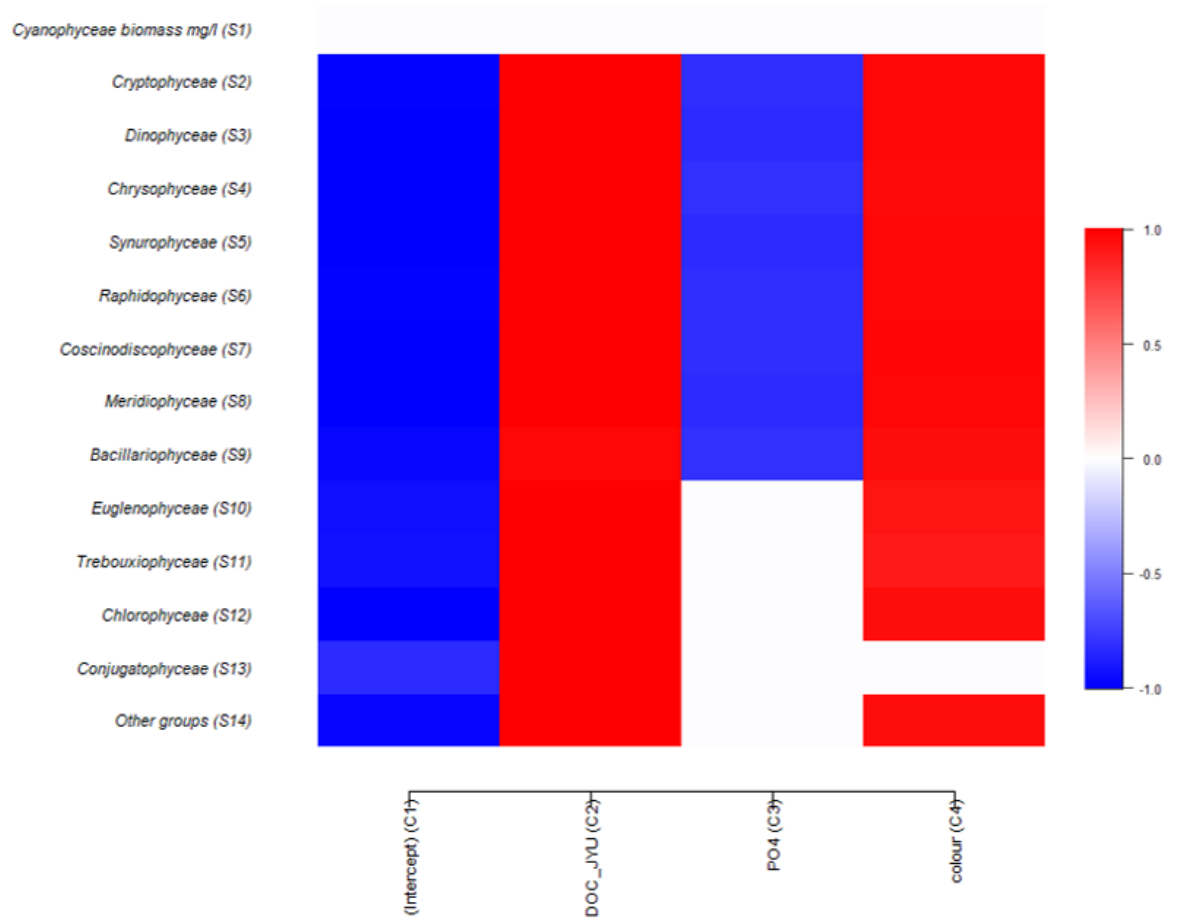

Figure 11: Effect of DOC, colour and PO4 on phytoplankton class abundance. Red = positive effect, blue = negative, white = no significant effect

4. Discussion

The main change in water chemistry in the study lakes in Finland during the last decades was a significant increase in water colour and temperature. Increasing trends of water colour and temperature have previously been shown in other regions in Finland as well (Vuorenmaa et al., 2006). This concurs with a global observed trend of surface warming and browning (O'Reilly et al., 2015; Garmo et al., 2020). Taking a closer look at the change in water colour, it looks like there was a steeper increase around the year 2000. Further statistical testing that is not a linear approximation of the data, could give more insight on the matter. Even in lakes which showed an overall decrease of water colour over the study period, this increase around the start of the new Millennium was seen. A similar increasing trend around that time was observed in Norwegian drinking water reservoirs. There, the trend was related to changes in precipitation patterns and changes in water pathways (Hongve et al., 2004), which is in accordance with the known processes that influence the concentration of organic substances in fresh water systems (Freeman et al., 2001, 2004; Pastor et al., 2003). In lake Päijänne, a

study in the years 2000 to 2014 also indicated an increase in TOC concentration. The increase was linked to a combination of climatic variables and atmospheric deposition and the TOC concentration was predicted to decrease in the future (Forsius et al., 2017).

Additionally to the increase in water colour and temperature, an increase in iron and a significant decrease in phosphate, nitrate and DOC as well as a decrease in TOC occurred. Decreasing trends in phosphate and nitrate have been observed globally (Garmo et al., 2020). TOC and DOC have been known to be positively related to water colour which is contradictive to the results in this thesis (Kortelainen, 1993; Underwood et al., 1998). However, other studies could not find a correlation between water colour and DOC as well (Lapierre et al., 2021). Water colour can also be the result of other variables than the concentration of organic carbon. When analysing the effect of the other hydrology variables on water colour, iron, TOC, and nitrate were positively related to water colour, while temperature and phosphorous were negatively related. Iron can precipitate in water in presence of manganese. This will result in a reddish water colour (bin Jusoh et al., 2005) and can further bind to the organic compounds. This in turn leads to an interference with the DOC reading by the carbon analyser and results in a higher value. However, it seems unreasonable that the increase in iron alone resulted in the different trend of water colour and organic carbon. More likely, the structure of the data was the cause of the conflicting results. The data had scarce measurements for DOC and those measurements were not collected consistently over time. A few lakes with low DOC values had been added during the end of the study period which could have skewed the results. The TOC values overall showed a decrease over time, but still TOC was positively correlated with water colour. Similary to the water colour values, TOC values also increased clearly around the start of the new millennium. Due to fluctuations and high variation in the data in the beginning of the study period, this trend might have been masked by the overall trend. Hence, water colour and TOC could have been positively related for part of the study period and there could be an increase of total organic carbon in the last couple of decades.

Species richness was increasing over the study period. Phosphate, colour, temperature and iron had a positive effect on species richness, while nitrate and TOC had a negative effect. Jeppesen et al. (2002) have found that shifts in phosphorous concentration result in shifts in the species community which could explain the positive relationship between phosphate and species richness. Contradicting to this thesis, water colour and temperature have been shown to have a negative effect on species richness (Eloranta, 1995; Urrutia-Cordero et al., 2017). However, other studies have stated that the interaction of temperature with other hydrological variables affects species richness positively. Warming in combination with a reduction of phosphorous was shown to increase heterogeneity in the water column in deep lakes which can promote phytoplankton species co-existence and richness (Pomati et

al., 2012). The response to a hydrological variable can also be non-linear. In a clear boreal lake, a threshold of DOC concentration was observed up to which DOC had a positive impact on primary production. After this threshold was reached, primary production was affected negatively by DOC concentration (Seekell et al., 2015).

Water colour and DOC are known to not only affect species richness but also species composition (Maileht et al., 2013; Lebret et al., 2018). The nestedness and turnover analysis in this thesis points out that lakes with an increase in water colour had a higher nestedness and lower species turnover than lakes with a decrease in colour. These results in the sample lakes indicate that with increasing water colour more of the original species pool stayed intact, while there was more species turnover with colour decrease. But overall, the nestedness for all lakes was low which indicates that most community changes were due to turnover. Hence, few species were found in both 1965 and 2015 and a lot of species were replaced by others during this time period. Another study on phytoplankton community composition observed that nestedness decreased over time which indicated that temporal variation could lead to heterogenisation of the phytoplankton community (Wojciechowski et al., 2017). Brownification may reduce this heterogenisation process in the study lakes by resulting in a higher nestedness of the phytoplankton communities. The temporal turnover in phytoplankton has been closely related to spatial turnover that is mainly caused by environmental variables (Zhang et al., 2018). Therefore, the temporal turnover could indeed be the result of changes in the environment, like brownification. Even though colour seemed to affect species composition, other variables had stronger effects on species composition, like temperature. The Simpson index used for the overtime analysis was a pairwise beta diversity index, which means, it only considered two time points due to the time constraint of this thesis. The index hence ignored all the possible changes that happened in the phytoplankton community within that time period. Yet, when comparing the analysis of all sample lakes to the analysis in lake Päijänne, similar results were shown. The analysis of lake Päijänne included more time points between 1965 and 2015. This indicates that analysing temporal data of one lake yields similar results to an analysis of spatial data including many lakes. However, the phytoplankton abundance data in the temporal data had been analysed by multiple people with differing effort and knowledge, so the spatial data could have less variation in the quality of species abundance data.

When only considering the spatial data set from the RNA-unit project, functionality and nutritional mode of the phytoplankton community changed with water colour, as flagellated and autotrophic species increased with increasing water colour. Flagellated autotrophic species have been shown to be dominant in high DOC concentrations (Deininger et al., 2017). Flagellated species have higher mobility which facilitates tracking of favourable conditions (Clegg et al., 2007). This could explain their higher abundance in dark coloured water, as they can avoid the low light conditions in the dark water

better. Reynolds (2006) tough, could not find a clear response of non-flagellated species to water colour. The results further indicated that mixotrophic species increased with low water colour but stagnated at darker water colours which resulted in a negative correlation between water colour and mixotrophic species. Mixotrophic species have been shown to have competitive advantages in red-light conditions (Luimstra et al., 2020). In polyhumic lakes with dark water colour, red light is the only light available at one-meter depth (Keskitalo & Eloranta, 1999c) and mixotrophic species should be less affected by the low light conditions because they are less dependent on light availability. In the upper more illuminated layers, mixotrophic species are outcompeted by autotrophic species (Lebret et al., 2018), which would indicate that an increase in water colour would benefit mixotrophic species abundance. However, the results of this thesis show no such trend. This could indicate that mixotrophic species are not inherently dominant in dark water, but the study did not have many lakes with a high colour number. Possibly mixotrophic species would be more dominant in the conditions that prevail in polyhumic lakes. Additional to colour, the other hydrological variables also affected the distribution of functionality and nutritional mode significantly.

The RNA-unit project dataset further indicated that water colour and DOC positively affected all phytoplankton classes, except for Conjugatophyceae. Similar results have been found for Cyanophyceae (Lenard & Ejankowski, 2017). Mixotrophic species, like Cryptophyceae, Dinophyceae or Raphidopyceae, are linked to polyhumic lakes (Urrutia-Cordero et al., 2017). These results are contradicting to the results from the functionality analysis of this thesis because many of the species in those phytoplankton classes are mixotrophic. The ratio of autotrophic to mixotrophic species was increasing with water colour which indicated that phytoplankton classes with a high number of mixotrophic species should have been negatively affected by water colour. However, the phytoplankton analysis considered phytoplankton classes that are rather broad and include both autotrophic and mixotrophic species. The classes of phytoplankton that are expected to thrive in polyhumic lakes may also include species that show the opposite behaviour which masks the expected trend. To predict the species composition more accurately, higher taxonomy levels could be considered.

Overall, water colour increased but it did not affect the phytoplankton community in the expected way. The most noticeable change in water colour and total organic carbon was around the start of this millennium. Since colour and DOC fluctuation are assumed to follow environmental influences (Pace & Cole, 2002), there could be environmental factors that induced the recent increase. Precipitation patterns and peatland decomposition were mentioned to be important variables for introducing organic carbon to freshwater systems (Freeman et al., 2004; Lenard & Ejankowski, 2017). Rain leads to higher water content in peatlands which results in carbon leaching into surrounding waters, so higher

precipitation frequency will also result in darker water colour (Lenard & Ejankowski, 2017). Additional to the peatland decomposition due to a warming climate, draining of peatlands also has an impact on decomposition. The draining causes higher aeration of the peatland that further results in higher decomposition rates (Minkkinen et al., 1998; Laine et al., 2013). The effects of climate change also are predicted to influence lake biodiversity, as species richness and biodiversity decrease with browning and higher temperatures (Urrutia-Cordero et al., 2017). However, this trend has not been observed in the study lakes of this thesis, even though there was an increase in water colour and temperature. The water chemistry variables might not have reached the critical threshold yet which would induce the predicted changes in the phytoplankton community. But if the trend of browning and temperature increase continues in the future, other changes in the phytoplankton community could be visible. With warming small autotrophic species are expected to be favoured (Rasconi et al., 2015), but also mixotrophic taxa like *Dinobryon* and *Cryptomonas* (Urrutia-Cordero et al., 2017).

Furthermore, many variables that also influence phytoplankton were not included in the thesis. Mixing conditions (Peeters et al., 2007) and the duration of ice cover (Beall et al., 2016) are examples of such variables. Nutrient load also affects the phytoplankton community (Elliott et al., 2006) but in this thesis, the included variables of phosphate and nitrate did not influence biodiversity significantly. High nutrient loads have been related to blooms of for example Cyanophyceae (Elliott et al., 2006), but the study lakes indicated a decrease of the nutrient load since 1965. Nevertheless, some of these unconsidered environmental variables could have a stronger effect on the phytoplankton community than water colour and could therefore be responsible for changes in the phytoplankton. Furthermore, the thesis did not include interactions of the hydrological variables, like phosphate and temperature, which could have had significant effects on species composition (Pomati et al., 2012). To make more conclusive statements on biodiversity and community compositions an experiment with a controlled input of all the hydrological variables could be considered.

4.1 Conclusion

In conclusion, water colour has been increasing since 1965, but in the last 20 years, a clear increase was observed in both water colour and organic compounds. The phytoplankton community in the study lakes did not change fully as expected. In the past decades, there was both an increase of species richness and a shift in community composition. However, it would be important to survey whether the recent changes in water colour will result in a shift in the phytoplankton community towards a community expected in polyhumic, warm lakes. So far, the expected conditions have not been reached in the study lakes yet and water colour can even have a positive effect on phytoplankton diversity. The master thesis, therefore, leaves open questions for further research. The reason for the water colour increase in the last 20 years would be important to know for further management decisions. Further

research on the phytoplankton community can help to get more clarity on their relationship to an increase of colour in lakes with low or middle colour values. The effect on the phytoplankton community is important because changes that concern the phytoplankton will affect the whole food web and lake ecosystem.

5. Acknowledgements

I would like to thank Satu Estlander, Kristiina Vuorio and Jukka Horppila for supervising this thesis and helping to understand the data and results. Special thanks to Kristiina Vuorio and SYKE and Marja Tiirola of the University of Jyväskylä for providing the data used in this thesis. I would further like to thank Otso Ovaskainen and Nerea Abrego for giving inputs on the statistical analysis.

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Appendix

Table 6: Changes in biodiversity in each lake

Sample site	Richness 1965	Richness 2015	Sorensen	Simpson	Nestedness	Difference in richness
Ähtärinjärvi Y9	69	57	0.88888889	0.87719298	0.01169591	-12
Äimäjärvi, Rastinselkä 1	136	37	0.90751445	0.78378378	0.12373067	-99
Alvajärvi	115	84	0.76884422	0.72619048	0.04265374	-31
Alvajärvi		91	1			91
Aurejärvi 2	27	54	0.85365854	0.77777778	0.07588076	27
Enäjärvi Rompsinmäki 5	101	30	0.81679389	0.6	0.21679389	-71
Hahmajärvi	31	57	0.72727273	0.61290323	0.1143695	26
Hauhonselkä,Valkkakivi 2	40	74	0.80357143	0.725	0.07857143	34
Hiidenvesi syvänne 90	76	38	0.84347826	0.76315789	0.08032037	38
Hirvijärvi 2 T	113	115	0.72807018	0.72566372	0.00240646	2
Ilomantsinjärvi 2	85	110	0.80512821	0.77647059	0.02865762	25
Inhottujärvi	14	72	1	1	0	58
Iso Löytäne	39	58	0.87628866	0.84615385	0.03013481	19
Iso Rautavesi	62	58	0.85	0.84482759	0.00517241	-4
Isojärvi 1	36	58	0.80851064	0.75	0.05851064	22
Jämsänvesi 23	73	90	0.7791411	0.75342466	0.02571645	17
Juojärvi 34.8	68	89	0.77070064	0.73529412	0.03540652	21
Jyväsjärvi 510	67	51	0.83050847	0.80392157	0.02658691	-16
Jyväsjärvi 510	67	100	0.88023952	0.85074627	0.02949325	33
Kankarinjärvi	49	78	0.93700787	0.91836735	0.01864053	29
Karankajärvi 1	40	64	0.76923077	0.7	0.06923077	24
Karhijä 3	94	82	0.88636364	0.87804878	0.00831486	-12
Karijärvi 015	39	76	0.79130435	0.69230769	0.09899666	37
Katumajärvi, syvänne 97	34	69	0.88349515	0.82352941	0.05996573	35
Keitele 33	52	73	0.824	0.78846154	0.03553846	21
Keitele 54	77	77	0.80519481	0.80519481	0	0
Keitele 55		72	1	1	0	72
Kermajärvi 28	57	75	0.78787879	0.75438596	0.03349282	18
Keurusselkä 113	77	77	0.85714286	0.85714286	0	0
Koitere 1 Juuansaari	57	59	0.75862069	0.75438596	0.00423472	2
KONNEVESI 33	75	66	0.77304965	0.75757576	0.01547389	-9
Konnivesi 025	43	66	0.79816514	0.74418605	0.05397909	23
Koskelovesi 4	79	98	0.8079096	0.78481013	0.02309948	19
Köyliönjärvi 8	123	52	0.81714286	0.69230769	0.12483516	-71
Kuhnamo 100	71	80	0.85430464	0.84507042	0.00923421	9
Kuivasjärvi	30	56	0.86046512	0.8	0.06046512	26
Kukkia Lehtisaarenselkä	84	98	0.75824176	0.73809524	0.02014652	14
Kuohijärvi, Matoniemi 1	48	66	0.84210526	0.8125	0.02960526	18
Kuorevesi, Vasikkainniemi	51	72	0.80487805	0.76470588	0.04017217	21
Kuusvesi 66	70	76	0.80821918	0.8	0.00821918	6
Kynsivesi 65	45	78	0.82113821	0.75555556	0.06558266	33
Längelmäv 102 Ponsanse	64	69	0.7443609	0.734375	0.0099859	5

Lannevesi	52	52	0.76923077	0.76923077	0	0
Lappajärvi etelä p 125	67	69	0.83823529	0.8358209	0.0024144	2
Lappalanjärvi syv 002	86	86	0.77906977	0.77906977	0	0
Lehijärvi, Kalkkonen 4	58	42	0.82	0.78571429	0.03428571	-16
Leppävesi 17/4	62	69	0.80152672	0.79032258	0.01120414	7
Liesvesi	52	61	0.82300885	0.80769231	0.01531654	9
Lohjanj. Aurlahti 53	68	66	0.80597015	0.8030303	0.00293985	-2
Lummenne 3	40	91	0.84732824	0.75	0.09732824	51
Mahlunjärvi 1	60	94	0.74025974	0.66666667	0.07359307	34
Mouhijärvi Löyttykivi	62	50	0.85714286	0.84	0.01714286	-12
Muuratjärvi Lietniemi	59	63	0.83606557	0.83050847	0.0055571	4
Muuratjärvi Lietniemi	59	81	1	1	0	22
Muuruejärvi 37	86	87	0.75722543	0.75581395	0.00141148	1
Näsijä N14 Palovesi	27	76	0.88349515	0.77777778	0.10571737	49
Nerkoonjärvi 1	27	58	0.90588235	0.85185185	0.0540305	31
Nerosjärvi, itäpää 1	96	91	0.79679144	0.79120879	0.00558265	-5
Niinivesi 62	68	92	0.7875	0.75	0.0375	24
Nuorajärvi 1	52	70	0.72131148	0.67307692	0.04823455	18
Ormajärvi, keskiosa 1	31	40	0.8028169	0.77419355	0.02862335	9
PÄÄJÄRVI, PÄÄ1	45	56	0.84158416	0.82222222	0.01936194	11
Päijänne 70, Ristinselkä	31	67	0.91836735	0.87096774	0.04739961	36
Päijänne 71, Vanhanselkä	36	45	0.85185185	0.83333333	0.01851852	9
Päijänne 740, Tehinselkä	46	46	0.84782609	0.84782609	0	0
Pajulanjärvi 2	41	71	0.82142857	0.75609756	0.06533101	30
PALOKKAJÄRVI 7	130	75	0.82439024	0.76	0.06439024	-55
PALOKKAJÄRVI 7	130	95	1	1	0	-35
Pankajärvi 21	68	72	0.75714286	0.75	0.00714286	4
Pieksänjärvi 039	101	124	0.80444444	0.78217822	0.02226623	23
Pielinen 2 Läpikäytävä	58	83	0.80141844	0.75862069	0.04279775	25
Pihlajavesi 27	50	79	0.79844961	0.74	0.05844961	29
Pitkävesi 1	65	82	0.76870748	0.73846154	0.03024594	17
Pyhäjärvi 57	53	75	0.796875	0.75471698	0.04215802	22
Pyhäjärvi 93 va93	75	53	0.8125	0.77358491	0.03891509	-22
Pyhäjärvi, Hiisivuori 1	60	41	0.86138614	0.82926829	0.03211785	-19
Pyhäjärvi, syvänne 88	49	34	0.87951807	0.85294118	0.0265769	-15
Pyhäselkä 9 Pyhäsaari	44	63	0.8317757	0.79545455	0.03632116	19
Pyhäselkä 9 Pyhäsaari	44	97	1	1	0	53
Rapojärvi 024	57	74	0.81679389	0.78947368	0.02732021	17
Retunen 31.2	58	68	0.79365079	0.77586207	0.01778872	10
Rikkavesi 26	62	60	0.78688525	0.78333333	0.00355191	-2
Ruotsalainen 81	48	80	0.796875	0.72916667	0.06770833	32
Ruov N18 Vähärengasniemi	30	79	0.85321101	0.73333333	0.11987768	49
Rutajärvi 1	89	83	0.75581395	0.74698795	0.008826	-6
Sääksjärvi Mois luod it	73	79	0.86842105	0.8630137	0.00540735	6
Saarijärvi 18	49	75	0.83870968	0.79591837	0.04279131	26
Salajärvi, Kirjussaari 1	101	65	0.81927711	0.76923077	0.05004634	-36
Saravesi 5	76	80	0.85897436	0.85526316	0.0037112	4
Summasjärvi 1	45	88	0.78947368	0.68888889	0.1005848	43

Suontee 1	51	82	0.81954887	0.76470588	0.05484299	31
Suvasvesi Vaahtovanselkä	95	95	0.78947368	0.78947368	0	0
Tarjannev 112	35	80	0.79130435	0.65714286	0.13416149	45
Toisvesi 110	38	63	0.86138614	0.81578947	0.04559666	25
Tuomiojärvi 1	128	77	0.80487805	0.74025974	0.06461831	-51
Tuusulanjärvi Opisto 26	84	46	0.86153846	0.80434783	0.05719064	-38
Unnukka Paloisselkä 8	94	70	0.74390244	0.7	0.04390244	-24
Uurainen	77	52	0.78294574	0.73076923	0.05217651	-25
Vanajav. Hopealinja 35	70	63	0.86466165	0.85714286	0.0075188	-7
Vaskiv 111	33	83	0.84482759	0.72727273	0.11755486	50
Vatianjärvi Repohiekka	73	83	0.79487179	0.78082192	0.01404988	10
Vehkajärvi 3		75	1			75
Vesijärvi, Enonselkä 79	78	58	0.88235294	0.86206897	0.02028398	-20
Viekijärvi 1	58	90	0.75675676	0.68965517	0.06710158	32
Vuohijärvi Kintuns 088	43	69	0.76785714	0.69767442	0.07018272	26
Vuosjärvi 51	85	81	0.79518072	0.79012346	0.00505727	-4